THE MORPHOLOGY OF THE MADREPORARIA, VI THE FOSSULA IN RUGOSE CORALS.[1]

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The term fossula, as employed in the literature of rugose corals, refers to a depression or pit in the calice, due to the smaller size of the septa at that particular region. Generally only one fossula is present in a corallite (Figs. 10 and 11), but there may be three (Figs. 1 and 12), or rarely two or four. The presence of the one or more pits gives a decided bilateral character to the calice, which otherwise might be perfectly radial.

The occurrence of one or more fossulæ has always been regarded as an important characteristic of the extinct Rugosa or Tetracoralla, nothing suggestive of such being found among modern hexameral Madreporaria, and, as would be expected, various explanations have been put forward to account for their presence. The present contribution is an attempt to understand the nature of the fossulæ from the stages passed through in the development of the individual corallite.

Where only a single fossula is present it is situated towards the ventral end of the principal axis of the calice, and where three occur the two additional are lateral and symmetrically disposed; when present the fourth fossula is towards the dorsal extremity of the principal axis. The single ventral fossula is the most persistent and characteristic of the series, and may be known as the main or cardinal fossula, or better, as the ventral-directive fossula, since it is associated with the cardinal or ventral septum. The two lateral are the alar fossulæ, and are dorsal to the alar septa; the fourth is the counter or dorsal-directive fossula.

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THE ALAR OR LATERAL FOSSULÆ.

We may first enquire into the nature of the alar or lateral fossulæ, as represented in the calice of a rugose coral such as *Ha-*

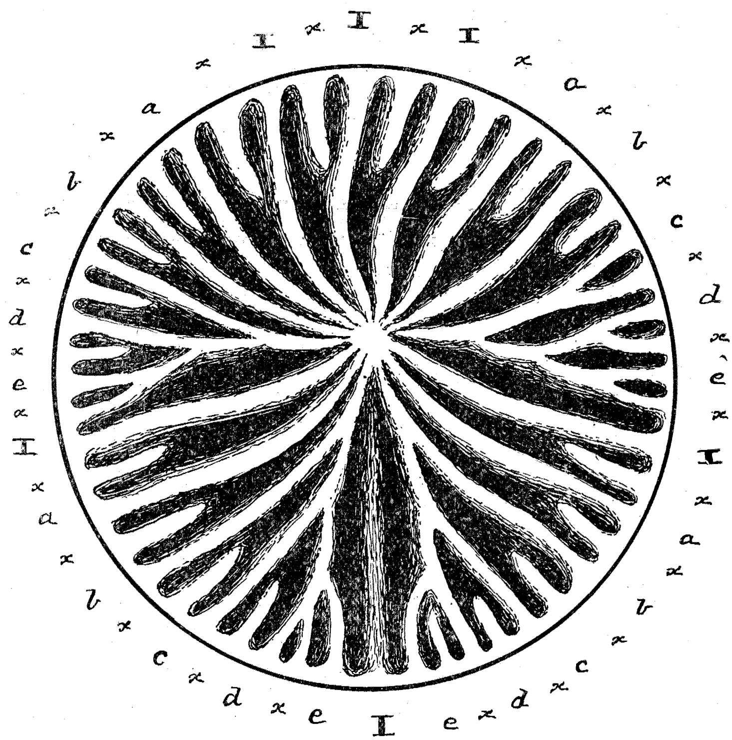

FIG. 1. Calice of *Hadrophyllum pauciradiatum*, E. & H., showing the arrange ment of the septa. Here and throughout the figures the Roman numerals I indicate the six primary septa or protosepta, the letters *a–e* the secondary septa or metasepta, and *x* the exosepta making up the outer smaller cycle (see description, Fig. 7); the lower side is regarded as ventral and the upper as dorsal. The two alar fossulæ are formed by the medio-lateral group of shorter septa, *c–e*, on each side, and the cardinal fossula by the ventro-lateral group of shorter septa, *b–e*, on each side, along with the more depressed ventral directive septum (I).

The series, Figs. 2–11, shows the complete septal development of *Streptelasma rectum*, Hall. The drawings were made as the successive stages were exposed on grinding down a corallite; the middle dotted line in each septum represents the line or centers of calcification.

drophyllum pauciradiatum (Fig. 1). The Devonian genus *Hadrophyllum* here chosen is one which Milne-Edwards and Haime,

in their "Coralliaires" (III., p. 334), specially distinguish as having three fossulæ, one axial and two lateral, and may therefore be taken as showing the alar fossulæ in their typical condition. In the figure given each alar fossula is seen to be associated with a few smaller septa (*c–e*) which fall short of the center, the shortening varying successively in a gradual manner. Further, each of the shorter septa is inclined dorsally by its inner border towards the next larger septum and is fused with it, so that together they form a group of septa very distinct from the perfect septa, and separated from the alar septum by a somewhat deeper and wider interspace.

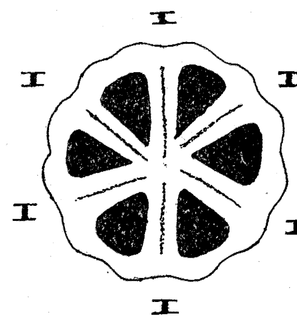

FIG. 2. Primary stage with six equal septa and six interseptal spaces or chambers. The axial septa are the dorsal and ventral directive septa, the former being the *Gegenseptum* and the latter the *Hauptseptum* of German writers; the four lateral septa are the dorso-lateral and ventro-lateral pairs, the latter being the *Seitensepta* or alar septa. The two middle interseptal chambers are the counter quadrants of palæontologists, and the two ventro-lateral are the principal or chief quadrants.

Frequently, however, between the primary alar septum and the group of incomplete septa on its dorsal aspect there is scarcely any special depression or pit present, such as is implied in the term fossula; even individuals of the same species vary much in this respect. Hence it will give a more precise morphological significance to the term if it be extended so far as to refer to the smaller, grouped condition of the septa, whether or not they are separated by a special depression from the alar septum. The subsequent discussion of the alar fossulæ will therefore have reference more to the group of smaller septa in this region than to any actual depression in the calice with which they may or may not be associated. Where the grouping occurs it is always a conspicuous feature of the calice.

The significance of the shorter septa associated with the alar fossula in *Hadrophyllum* can be understood by comparing the series of figures (Figs. 2–11) representing the complete septal development of *Streptelasma rectum*, as revealed by successive sections of a

single corallite.[1] It is seen that each alar or lateral region is that at which new septa (*a–e*) are successively added to the primary six. Furthermore, the additions take place in such a manner that the newer, shorter septa are for some time inclined towards the older, and are fused with them in a unipinnate manner by their inner borders; it is only towards the close of development (Figs 10, 11) that all the septa become free, and are then radially arranged. This inclination and fusion of the newer with the older septa, as well as their smaller size, gives a distinctive character to the alar regions in *Streptelasma* during the various developmental stages, and usually results in a special interval or interseptal space on the dorsal side of each alar septum.

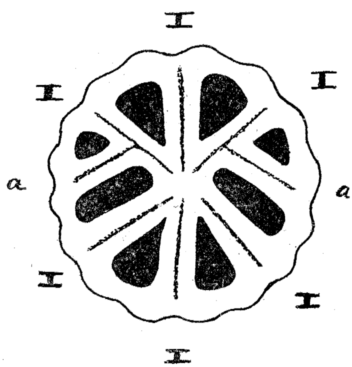

FIG. 3. A bilateral pair of metasepta (*a*) has appeared, a member within each of the middle chambers or counter quadrants, inclined towards its corresponding dorso-lateral primary septum.

If now the alar regions of Figs. 2–10 be compared with those of Fig. 1, the two alar fossulæ in *Hadrophyllum* are seen to correspond with the two lateral regions of addition of new septa in *Streptelasma*, and both are within the two middle of the six primary interseptal chambers. Hence each alar fossula in the adult corallite of *Hadrophyllum* really corresponds with ontogenetic stages in the establishment of the septa in *Streptelasma*, the septa concerned being those immediately dorsal to the primary alar septum.

That no alar fossula is present at the more mature stages of *Streptelasma* (Figs. 9–11) is due to the fact that as the coral attains its full development the septa become free from one another at their inner border, and at the same time become equal in size

[1] The septal sequence here illustrated is in accordance with Kunth's well known law of septal development found to be characteristic of the Rugosa. Hitherto, it has been generally assumed that only four primary septa are present in tetracorallids whereas six actually occur. However Haeckel's term Tetracoralla has still an appropriateness since the subsequent septa are formed within only four of the six primary interseptal chambers in contrast with the six in Hexacoralla.

and situated at equal distances apart, thereby presenting a more truly radial disposition. On the other hand in the mature corallite of *Hadrophyllum* the septa of the alar region do not reach the radiate condition; they retain their unipinnate arrangement throughout, and, as a consequence, the alar regions remain sharply separated from the rest of the corallite both by a special arrangement of the septa and by an interval.

The series of sections of *Streptelasma* further proves that the alar fossula is situated on the dorsal side of the alar septum; the latter takes no direct part in forming the depression, but merely constitutes its ventral boundary. As shown in Fig. 2, the right and left alar septa are the ventro-lateral pair of the six primary septa, and all the additions in the middle interseptal chambers necessarily take place dorsal to them. In sections the new septa are inclined by their inner border towards the dorso-lateral pair of primary septa, and are thus more nearly parallel with the ventro-lateral (alar) septa.[1] Sometimes, as in *Anisophyllum agas-*

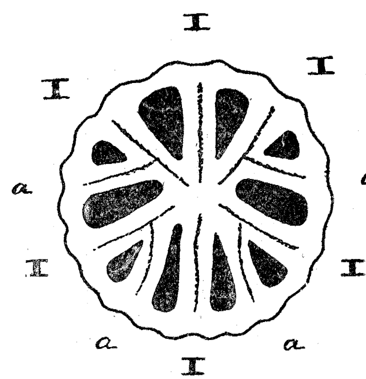

FIG. 4. A stage a little beyond that in Fig. 3. A corresponding pair of septa (a) has appeared within the two ventro-lateral chambers or principal quadrants, each member inclined towards a ventro-lateral (alar) primary septum.

[1] In giving the septal plan of a tetracorallid as viewed from above Delage & Hérouard ("Traité de Zoölogie Concrète," II^2, p. 692, Fig. 973) project the newer septa of the principal quadrants upon the cardinal septum and parallel with the alar septa, while those in each counter quadrant are projected upon the alar septum and are parallel with the dorsal directive or antipodal septum. The figure of *Hadrophyllum* here given, and also those showing the septal development of *Streptelasma rectum*, prove that this is not the true relationship of the inner ends of the metasepta within the calice. In each quadrant the inner end of each septum is from its origin directed towards the next older member of its own series. I have met with no instance in which the later developed septa are inturned towards and fused with the alar and axial directive septa, as seems to be usually assumed from the appearances presented by the external ridges and grooves alone. The explanation which Bourne gives (Lankester's "Treatise on Zoölogy," Art. Anthozoa, p. 73, Fig. 35) of the schematic representation of the septa of a zaphrentoid coral is manifestly self-contradictory as regards the sequence.

sizi, E. & H., the alar septa are much larger than any subsequently developed, and may thus emphasize the fossula adjacent to them. On the other hand, it is very doubtful if the alar septa themselves are ever smaller than the other principal septa, or are situated within the fossular depression, as is sometimes assumed in palæontological works.

Alar fossulæ of a like nature with those in *Hadrophyllum pauciradiatum* have been studied in other tetracorallids, especially in *Microcyclus discus*, Meek & Worthen, *Anisophyllum Agassizi*, E. & H., and also in *Hadrophyllum glans* (White). In these there is the same grouping of successively smaller septa, giving to the alar region its distinctive character. A still larger number of zaphrentoid corals, however, are found to resemble *Streptelasma rectum*:[1] during the earlier stages of development their new septa are related one to another just as they are in the adult of *Hadrophyllum*, while on approaching maturity they become equal and more strictly radial; they all, in fact, pass through a *Hadrophyllum* stage.

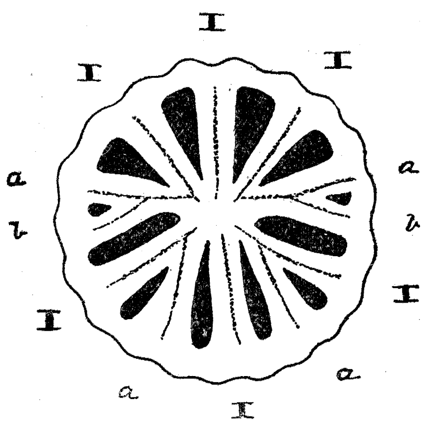

FIG. 5. A second pair of septa (*b*) is now present, one in each of the middle chambers, inclined towards the metasepta (*a*).

The true morphological significance of the difference between adult forms like *Hadrophyllum* with alar fossulæ and others like *S. rectum* in which they are wanting is thus only ontogenetic. In the one development does not proceed sufficiently far as to establish approximate radial symmetry, and the adult corallite

[1] It may be well to state that in the course of the investigations the septal development has been followed by means of serial sections in various species of the following genera comprised within the families Cyathaxonidæ, Palæocyclidæ, and Zaphrentidæ, namely, *Cyathaxonia*, *Duncanella*, *Palæocyclus*, *Hadrophyllum*, *Microcyclus*, *Streptelasma*, *Zaphrentis*, *Lophophyllum*, and *Anisophyllum*. Representatives of the families Cyathophyllidæ and Cystiphyllidæ, particularly the colonial forms, are found to be unsuitable for such studies.

retians the bilaterality of development of its septa; while in the other the bilateral symmetry of growth becomes replaced by a radial disposition of the parts. Whenever alar fossulæ are present they represent an incompletion in the establishment of the newer septa of the alar region, as compared with species in which no alar fossulæ are represented; they have only a developmental significance, and would not correspond with any structural peculiarity of the fully developed polyp. As would naturally be expected from such an explanation even individuals of the same species may vary much with regard to the presence or absence of alar fossulæ. In the calice of some specimens of *Microcyclus discus*, for example, there is a distinct grouping of the alar septa,

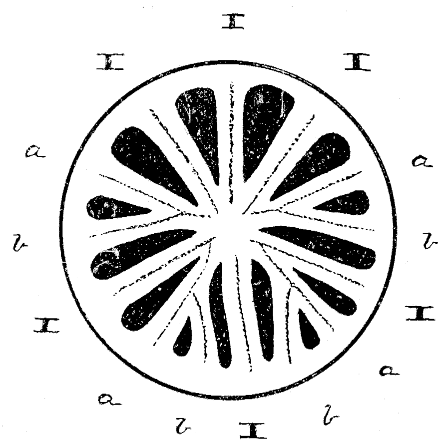

FIG. 6. A corresponding second pair of septa (*b*) has appeared within the ventro-lateral chambers.

while in others the septa have become perfectly radial, and no alar region is distinguishable.

The alar fossulæ represent regions where new septa are being added, and the interspaces may reasonably be expected to be different from the other septal interspaces, and likewise to vary at different stages according as the new septa are just appearing or are nearly fully developed.

From developmental studies the conclusion is thus reached that in all ordinary species of zaphrentoid corals the septa of the alar region pass through a fossular stage as here understood,

whether or not the adult arrangement be radiate; or, stated in another way, the presence of alar fossulæ in an adult corallite is a retention of a developmental characteristic.

THE CARDINAL OR VENTRAL FOSSULA.

Enquiry may now be directed into the nature of the cardinal or ventral-directive fossula. This is the most important of the series, being usually represented in mature calices even when all traces of the alar fossulæ have disappeared. Further, its constitution is by no means so simple as that of the alar fossulæ.

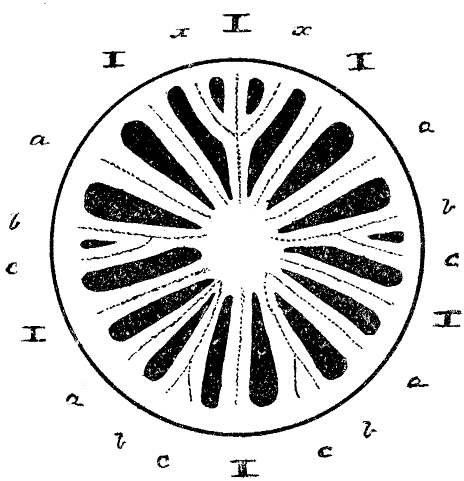

FIG. 7. A third additional metaseptal pair (c) has appeared within both the middle and ventral chambers, the middle pair developing first. A pair of septa (x) has also appeared, one within each of the dorso-lateral primary chambers, fused with the dorsal directive. In relation to the polyp the septa which appear midway between the principal septa are exosepta, and always constitute the outer, smaller cycle in the mature calice; the larger septa, constituting the inner larger cycle, include both the protosepta and metasepta, and are entosepta.

As represented in *Hadrophyllum* (Fig. 1) the cardinal fossula is associated with two groups of successively shorter septa (b–e), a group being situated on each side of the cardinal or ventral directive septum, and, in addition, the cardinal septum (I) is itself smaller than the other fully developed principal septa. The members of each ventro-lateral group of smaller septa (b–e) are related to one another in the same manner as are the members

in an alar fossular group (*c–e*), that is, the shorter septa are turned towards the successively larger, and are united with them by their inner ends in a unipinnate fashion. In general also the space on each side between the group of newly added septa and the axial septum is greater than the other septal interspaces and more pit-like.

Again comparing the adult calice of *Hadrophyllum* with the developmental series of sections of *Streptelasma* in Figs. 2–11,

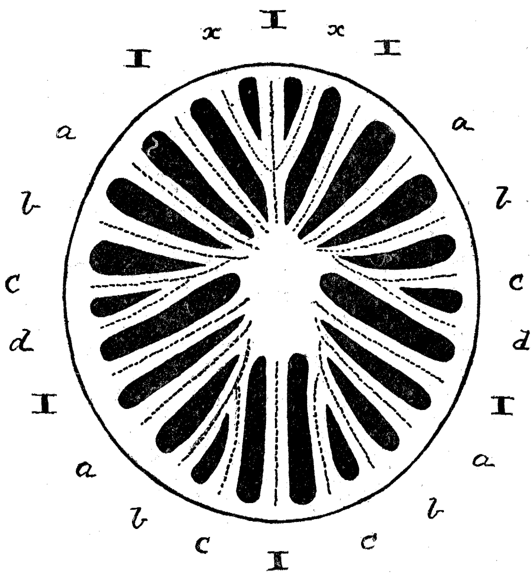

FIG. 8. A stage somewhat in advance of that in Fig. 7. An additional septum (*d*) is present in each middle chamber, while the two pairs, *c*, are much larger. The section shows very clearly the inclination of the septa towards each other in the alar and ventro-lateral regions, only the oldest septa reaching the columella (cf. Figs. 1 and 12).

it is seen that the fossular region on each side of the cardinal septum is a region where the addition of new septa takes place, just as is that on the dorsal aspect of each alar septum. Likewise, the new ventral septa in *Streptelasma* are inclined towards the older and fused with them until the mature condition is reached, when they become free, of the same size as the others, and more nearly radially arranged (Figs. 10, 11). Therefore the cardinal or ventral groups of shortened fused septa in *Hadro-*

phyllum represent a developmental stage when compared with the mature condition of such a form as *Streptelasma;* as in the case of the alar fossulæ, a developmental stage in *Streptelasma* persists as the adult condition in *Hadrophyllum.* The axial cardinal fossula of *Hadrophyllum* is thus shown to be associated with two groups of incompletely developed septa, a group on each side of the cardinal directive septum, while at the same time the latter is much smaller than the other primary septa. Such a

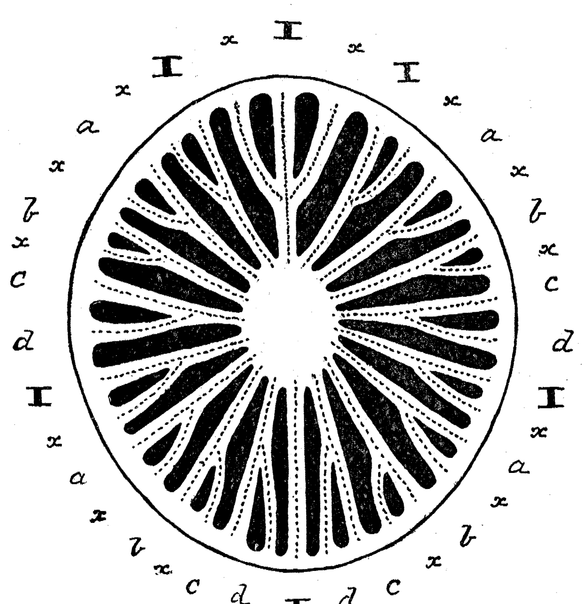

FIG. 9. Exosepta (x) have now appeared in association with most of the fully developed septa, namely, all the protosepta (except the ventral directive) and the metaseptal pairs a and b. The exosepta are at first turned towards and fused with their corresponding dorsal entoseptum.

fossula as a whole may be spoken of as compound, while those in the two alar regions are simple fossulæ.

Studies on other species of rugose corals show that throughout the group the cardinal fossula in the adult calice is constituted either on the *Hadrophyllum* or *Streptelasma* plan; rarely, as in *Anisophyllum*, the cardinal directive septum is much larger than the other primary septa and then the fossula is really double, a

depression on each side of the large axial septum corresponding with the smaller, newly added septa.

As shown in the various figures the cardinal or ventral-directive septum is smaller than the other principal septa, and remains thus when all the other septa have become equal; the axial fossula is then represented in the fully developed calice by the smaller cardinal septum alone, without a special lateral depression on

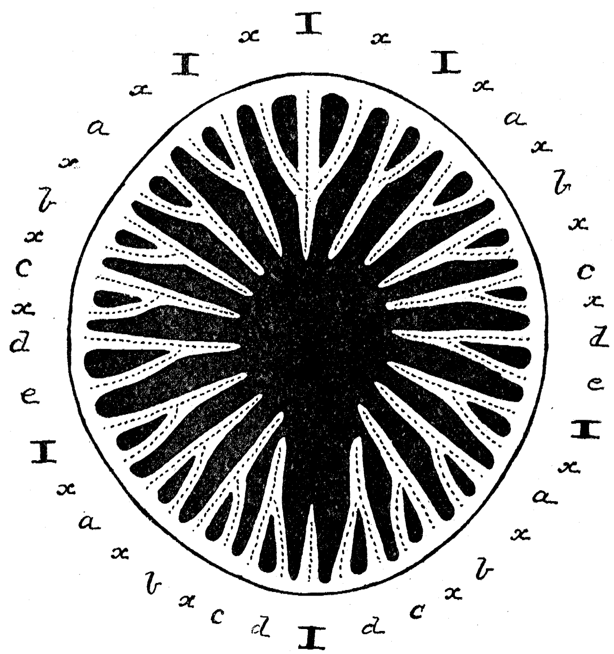

FIG. 10. Section towards the upper part of the corallite. The septa are now free from the columella, and the ventral directive septum is smaller than the others. More exosepta and metasepta have appeared than in Fig. 9, each exoseptum being still fused with its corresponding entoseptum.

each side. Such a condition clearly calls for a different explanation from that given for the alar fossulæ, or for the lateral parts of the cardinal fossula; these have been found to correspond with ontogenetic stages of species which attain nearly perfect radiality in the adult, while the ventral-directive septum in most instances remains shorter even within the mature calice. Manifestly the small directive septum must correspond with some

peculiarity in the polyp itself, an axial peculiarity situated towards the ventral side.

In a paper already published (*Ann. & Mag. Nat. Hist.*, May, 1902), I have given good reasons for supposing that of all modern Anthozoa the living Zoantheæ are most nearly related to the extinct Rugosa. In zoanthids the mesenteries beyond the primary six are added in such a manner as would give the septal sequence characteristic of the Rugosa, that is, the sequence

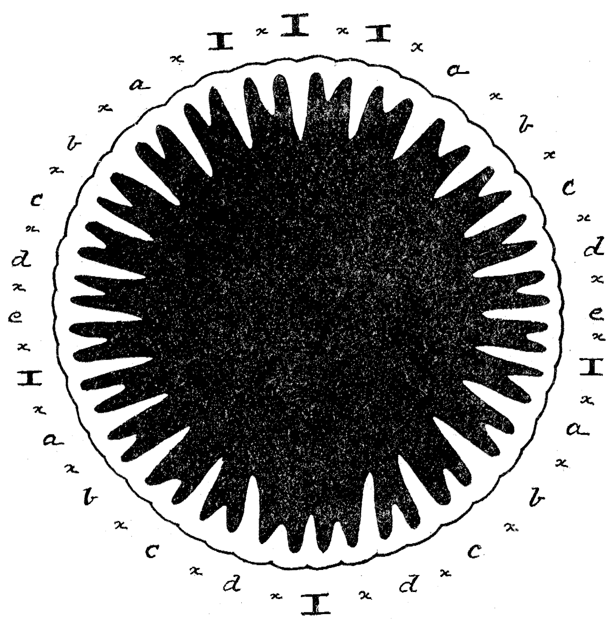

FIG. 11. A section near the upper limit of the corallite. All the septa are now more strictly radial, and those of the inner and outer cycles regularly alternate. There is no distinction in size between the six protosepta (I) and the various meta-septa (*a–e*), except as regards the ventral directive septum, the smallness of which gives rise to the simple axial fossula.

represented in Figs. 2–10; the only difference is that in modern zoanthids the new mesenteries are added within only the two ventral of the six primary chambers, whereas in the rugose polyps they were added within four of the six primary chambers — the ventral and middle pairs. This difference is, however, but one of detail compared with the actual order of development

of the mesenteries and septa. It is the manner of appearance of the septa beyond the primary six which separates the Rugosa from modern hexameral corals, a separation of the same significance as that by which zoölogists distinguish cyclic hexameral actinians from zoanthid polyps.

The presence of the smaller axial septum in the cardinal

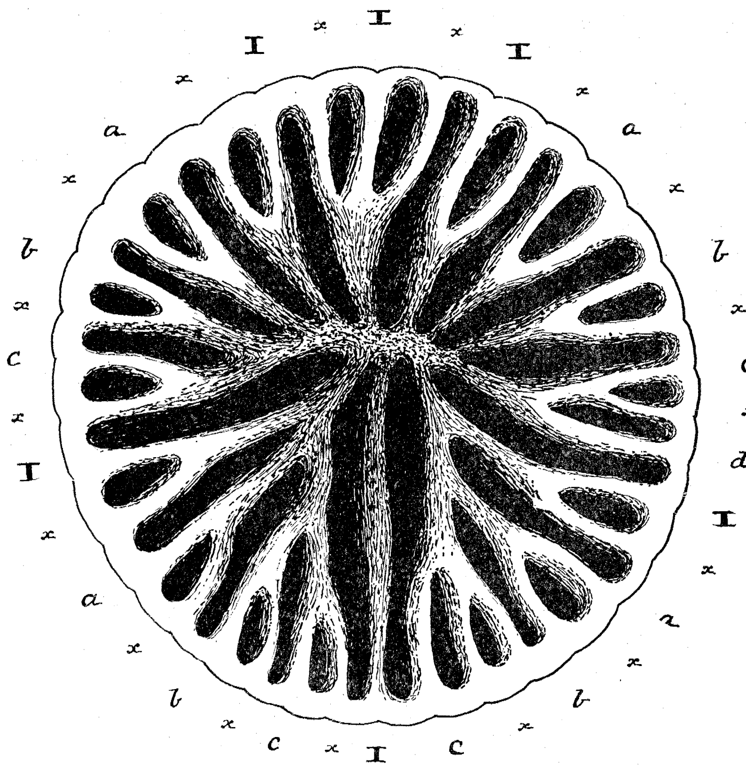

FIG. 12. Arrangement of the septa in a young corallite of *Streptelasma profundum* (Owen). At this early stage the septa are arranged in a manner very similar to those in the mature corallite of *Hadrophyllum* (cf. Fig. 1), while in the fully developed corallite they are nearly radial. The septa show a slight inequality in number on each side, a condition also usually met with in recent zoanthid polyps.

fossula of the Rugosa serves to confirm in a peculiarly direct manner the relationship of the group to the living Zoantheæ. As is well known, one of the characteristics of the zoanthid polyp is the occurrence of a single gonidial groove, sulcus, or siphono-

glyph along the ventral extremity of the stomodæum, as compared with the two opposite grooves (dorsal and ventral) usually present in hexactinian polyps. The single groove in zoanthids is usually well-developed, and its walls often project for some little distance within the ventral directive entocœlic chamber, and are frequently continued into the polypal cavity beyond the rest of the stomodæal wall. It is strongly ciliated and is concerned chiefly in the circulation phenomena of the polyp, sometimes remaining open when the mouth is otherwise closed by the approximation of the lips.

The occurrence of the single gonidial groove gives a marked contrast to the two extremities of the stomodæum of zoanthid polyps, and a decided bilateral character to transverse sections. Manifestly it is the presence of just such a structure which we should expect to result in a diminution of the axial septum were a skeleton formed beneath it; indeed, with such a stomodæum, having a groove at one end and not at the other, we could scarcely expect that the two extremities of a corallite would be alike. In the absence of the rugose polyp itself, no surer proof of the relationship of the group to the zoanthids could to my mind be adduced than that which admits of the correlation of the simple cardinal fossula with a ventral stomodæal groove.[1]

On the above explanation it may reasonably be asked why no corresponding axial fossulæ are found in the calices of recent corals. In answer to this it can be affirmed that as yet we have no certain instance of the presence of a gonidial groove in the stomodæum of modern coral polyps. In the polyps of over thirty species of West Indian corals which I have examined there was no evidence of such a groove, and the same can also be said of a like number of Pacific corals. The stomodæum of coral polyps is comparatively short, and presents the same histological structure all round, showing there is very little if any physiologi-

[1] Other evidences of bilaterality and axial differentiation are sometimes presented by zoanthid polyps. In living examples of *Zoanthus* the axial tentacle over the ventral directive entocœle is frequently larger than any of the others; sometimes the coloration along the dorso-ventral axis is different from that elsewhere; and I have also found the disc to be actually grooved or depressed along the axis. The Ceriantheæ are also characterized by the possession of a single siphonoglyph, but the manner of addition of the mesenteries in this group precludes any relationship with the Rugosa.

cal differentiation associated with its extremities. In this respect living coral polyps differ from the closely allied skeletonless hexactinians, where a gonidial groove usually occurs at each extremity of the stomodæum.

An examination of other species of rugose corals demonstrates that the cardinal fossula is somewhat similarly constituted throughout the group. The two extremes of its development are the complex condition met with in forms like *Hadrophyllum* and the simple modification present in the mature calice of *Streptelasma*. In the one we have it associated with a grouping of incompletely developed septa on each side of a feebly developed axial septum, while in the other it is represented by the smaller axial septum alone. The fossula in the first has an ontogenetic as well as a morphological significance, while in the second it is correlated with a structural peculiarity of the mature polyp. In zaphrentoid corallites in which the calcareous material has been replaced by silica, and the septa are exposed throughout their vertical length,[1] the entire series of developmental changes undergone by both the alar and the cardinal fossulæ can sometimes be observed at a glance, confirming the results obtained from a series of sections like that shown in Figs. 2–11.

The condition in rugose corals with the newly added septa arranged bilaterally in four groups, distinct from the other septa, I propose to term the *Hadrophyllum-stage*, since it is so characteristically displayed in this genus. In general it will be associated with three fossulæ. In its significance the stage is comparable with that of the *Edwardsia* or *Halcampa*-stage met with in some mature actinians and the polyps of modern corals, and passed through in the ontogeny of others. All the simple Rugosa, namely those embraced within the group Zaphrentoidea, exhibit the *Hadrophyllum*-stage for a longer or shorter period during their development; in some it is retained at maturity, while in others it is replaced by a more nearly radial condition of the septa.

[1] For beautifully perfect silicified specimens of *Streptelasma profundum* (Owen), with all the interseptal matter removed by decalcification, I am indebted to Prof. F. W. Sardison, and for others from the geological collections of the University of Michigan to Prof. I. C. Russell. For many other species of Rugosa from the National Museum I am under obligations to Prof. C. Schuchert, and from the British Museum to Dr. F. A. Bather.

The ontogeny of the various forms shows that the shorter septa associated with the fossulæ cannot be considered as representing a cycle or cycles different from the others. Polycycleism, as we know it in the hexacorallids, does not occur in the tetracorallids; however many septa may be developed there are only two cycles represented, the inner larger septa being entosepta while the outer shorter are exosepta. The entosepta include the six primary protosepta and the later metasepta, some members of the former being at times larger than the rest (*Anisophyllum*). In *Menophyllum* the metasepta formed within the middle and ventral chambers differ greatly in size, those in the two ventral chambers being the larger. In this genus three fossulæ are said to occur, the two lateral situated as before on the dorsal aspect of the alar septa; the alar septa are not, as is generally assumed, included within the fossula itself.

As stated in the introduction, a fourth or dorsal-directive fossula is sometimes present in rugose corals, but this occurs very rarely, *Omphyma* being given as an example. Among a collection of *Zaphrentis compressa*, E. & H., from Spergen Hill, Indiana, I have found several in which there is in the mature corallite a conspicuous fossula towards both the dorsal and ventral extremities of the principal axis, the ventral fossula being the more pronounced. In the majority of specimens, however, there is no hint of the dorsal pit. The dorsal fossula would appear to have no developmental significance, since the septal arrangement is there the same as in other species of this genus; rather, it would seem to correspond with some peculiarity of the adult stomodæum, perhaps with the longer continuation of its dorsal extremity.

Radial and Bilateral Symmetry.

A comparison of rugose corals having bilateral symmetry with those in which all the septa are radially arranged introduces considerations with regard to symmetry in corals generally. Mature corals and actinians, like most cœlenterates, are characterized by a more or less perfectly radial symmetry as regards their mesenteries, tentacles, and septa, yet throughout the course of their development these organs follow a decided bilateral method, both in the earlier and later stages.

So far as concerns modern corals I have lately shown (BIOL. BULL., July, 1904) that the septa, correlatively with the mesenteries, present very marked bilateral phases during nearly the whole of their ontogeny; it is only as the organs attain maturity that they become radially symmetrical.

Likewise the study of the development of a large number of rugose corals by the method of grinding proves that they are all characterized by a bilaterality of growth after the protoseptal stage; in the majority of species the bilaterality passes into a radial stage, but in some it is retained at maturity. The bilaterality of the Rugosa is however of an altogether different nature from that of modern Madreporaria; the septa in rugose corals are added as bilateral pairs at only four regions of growth, two on either side, whereas in modern corals the additions are made all round the periphery within the six primary interseptal spaces. Notwithstanding these developmental differences a more or less radial symmetry is reached by the adults of both groups. Little or no importance is thus to be attached to the old distinction that the Rugosa are bilaterally symmetrical while recent corals are radial; the species of both are ontogenetically bilateral, and the degree of radiality attained by the adult varies much in forms otherwise closely related, or even in individuals of the same species. Developmental bilaterality and mature radiality are just as much a feature of the extinct Tetracoralla as they are of recent Hexacoralla.

The more or less perfect radiality of the different groups of the cœlenterates as a whole is reached from very different developmental conditions, as can easily be seen from a survey of what is known with regard to the early stages of the organs in the scyphomedusæ, actinians, zoanthids, cerianthids, and recent and fossil corals. It follows that the adult radiality of organs which arise in such widely divergent manners in no way implies morphological relationship among the animals possessing them. Rather, it is an adaptation to the uniformity of environmental influences on all sides to which sessile or floating organisms are subject. The manner in which the organs arise seems immaterial; however varied the origin the same end is attained at maturity. The feature in the Rugosa here sought to emphasize

is that while the majority pass through their bilateral developmental stages and attain practical radiality, some retain the early bilaterality, evidenced by the presence of one or more fossulæ, The single stomodæal groove of the polyp, correlated with an axial fossula in the skeleton, is the only deep-seated character uninfluenced by the equality of the environmental influences, and usually precludes the attainment of perfect radiality among the Rugosa.

Why should certain rugose corals when mature retain the developmental bilaterality of the *Hadrophyllum*-stage while others continue their growth until their septa attain the radial condition? The former has been shown to be an early ontogenetic stage of all forms, hence rugose corals with alar fossulæ and a compound cardinal fossula are at a lower developmental stage than those attaining radiality. How far the differences are chronological seems uncertain, for some of the earlier Rugosa are as nearly radial as their later representatives, and the adult *Hadrophyllum*-stage was apparently no more common in earlier than in later Palæozoic times. According to Zittel ("Text-book of Palæontology," *Eng. Ed.*, p. 74), the distribution of certain genera characterized by a well-marked *Hadrophyllum*-stage is as follows: *Baryphyllum*, Devonian; *Hadrophyllum*, Devonian; *Anisophyllum*, Ordovician to Devonian; *Menophyllum*, Carboniferous Limestone; *Microcyclus*, Devonian. Others having a more nearly radial disposition of the septa in the adult are distributed in time as follows: *Streptelasma*, Ordovician to Carboniferous; *Zaphrentis*, Silurian to Carboniferous; *Cyathaxonia*, Carboniferous Limestone; *Duncanella*, Silurian; *Palæocyclus*, Silurian. Obviously both forms of corallite, bilateral and radial, were living together during the greater part of the Palæozoic age.

When the majority of trifossulate zaphrentoids are compared with the radial forms, the former are seen to be short, flat, or trochoid corallites, the latter long and conical; also the trifossulate species are usually smaller and have a fewer number of septa. It would seem that corallites with considerable vertical height have had the opportunity, as it were, to outgrow their developmental bilaterality, and their septa have assumed the radiality of maturity, while this has not been the case with the short flat

forms; wherever continuous vertical growth takes place, without the addition of new septa, radiality tends to be assumed by the septa already formed. In elongated forms a considerable vertical interval occurs between the insertion of each new bilateral pair of septa and an approximate radiality is attained, to be again destroyed on the addition of another pair. Somewhat similar changes have been shown to be also characteristic of the growth of modern hexameral corals; the developmental stages are bilateral, but between one stage and another an approximate radiality is reached. As regards the Rugosa it may be accepted as a general rule that developmental bilaterality at maturity is associated with shortness of calicular form.

It does not appear from systematic works that the presence or absence of fossulæ has proved to be a character of much taxonomic value. It is conceivable that forms otherwise closely allied may vary as to whether or not the septa at maturity attain the radial arrangement. The facts already adduced prove, however, that in any series of closely allied forms those with well marked fossulæ represent an earlier phylogenetic stage than those attaining radiality, but beyond this it does not yet seem possible to go.

Explanation of the Fossula.

Concerning the significance of the fossulæ the view here maintained is that they are due to two distinct structural features: (1) a grouping of smaller incompletely developed septa at the region of growth within the middle and ventro-lateral pairs of the six primary interseptal chambers (counter and principal quadrants); (2) in the case of the cardinal fossula only, a smaller ventral directive septum correlated with the presence of a single stomodæal groove in the polyp. The alar fossulæ are altogether the result of the first condition, while the cardinal fossula is either dependent upon a combination of both the first and second causes, or is entirely due to the second. Exceptionally, as in *Anisophyllum*, the cardinal fossula is due only to the first, when it appears as a double depression.

Other explanations of the origin of the rugose fossulæ have been offered. The view hitherto generally accepted is that which regards them as a sort of chamber for the hypertrophied mesen-

teries bearing the sexual products of the polyp. This was first suggested by Moseley (*Q. J. M. S.*, XXII., p. 394), from his studies of the living coral *Seriatopora*, in the following words: "The presence of the deep pits in *Seriatopora* for the reception of the single pair of generative mesenteries and their hypertrophied mesenteries may possibly explain the pits occurring amongst the septa of some palæozoic corals which may have had a similar function."

This theory has met with general acceptance only among English writers, particularly Nicholson, Ogilvie, and Bernard. It is founded entirely upon conditions met with in the modern *Seriatopora*. In the polyps of this genus, only the six primary pairs of mesenteries are present, the first developmental pair being by far the largest and bearing the gonads. In other corals, *e. g.*, *Pocillopora*, *Porites*, and *Acropora* (*Madrepora*), a like inequality, though to a less degree, is met with wherever only the six primary mesenteries occur, but as further cycles of mesenteries appear the six primary pairs become equal and are all fertile; moreover, in zoantharian larvæ the first pair of mesenteries often greatly exceed the others in the extent of their development. As regards their mesenteries the adult polyps of *Seriatopora* are merely at an early phylogenetic stage, and the skeletal pits are correlated with this. Our knowledge of the Anthozoa as a whole gives no support whatever for thinking that any of the mature rugose polyps had only two or even only a few reproductive mesenteries. Rather, the large number of principal or first cycle septa occurring in rugose corals, all more or less equal, gives good reason for assuming that a correspondingly large number of mesenteries would be fertile, as in the polyps of recent Zoantheæ, and also that such fertile mesenteries would be distributed all round the polyp. Moreover, Moseley's suggestion would explain only the occurrence of the pair of deep pits, one on each side of the primary septum; it would not account for the smallness of the axial septum itself.

Bernard[1] (1904, p. 10), while accepting that the use assigned

[1] Bernard, H. M., "The Prototheca of the Madreporaria, with Special Reference to the Genera Calostylis, Linds., and Moseleya, Quelch," *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XIII., Jan., 1904.

the fossula, as a sort of crypt for the sexual products, is probable enough, considers that this need not have been the cause of its origin. Rather, he would explain its presence on the mechanical assumption that at an early stage in its development the coral falls over, and in recovering the upright position the soft polypal parts detach themselves from the base of the prototheca in such a way as to bag down, and thus produce a pit or depression on the floor of the calice. Bernard thus expresses it: "The fossula has a very simple explanation, if the assumption of the falling over is correct. As the soft parts detach themselves from the base of the prototheca they might be expected to bag down, and they will continue to be acted upon by gravitation and drawn over towards the convex side of the coral until the vertical position has been regained. It is possible that this bearing over to the side may be due to the efforts of the polyp itself to bend up, but gravitation in a *causa efficiens.*"

Such a purely mechanical explanation is very unsatisfactory when we consider how hypothetical is the conception of any general falling over of the prototheca, and also of the influence which this would have upon the polyp itself as well as upon the corallite; it is difficult to conceive of the bagging down of the polypal tissues always at a definite region of the calice on each side of the cardinal septum. The view which I have submitted above, that the simple cardinal fossula is correlated with the presence in the living polyp of a gonidial groove or siphonoglyph, is more in harmony with the facts of anthozoan morphology, while there can be no question as to the significance of the grouping.

Bernard fails to see the evidence for the existence of more than one true fossula in any coral examined by him. He finds this usually on the convex or "dorsal" side, this being the side which I have here termed ventral, as being more in agreement with the accepted anthozoan terminology. The occasional presence of the fossula on the concave side he attempts to explain as dependent upon a shallower more open prototheca than that in which it forms on the convex side.

Some of Bernard's other statements seem so contrary to all that we know of the nature and development of the Rugosa that

I refer to them here, although not directly bearing upon the fossula. He makes the supposition (p. 11) that "The falling over of the prototheca will explain the departure from a strictly radial symmetry of the septa seen in these curved Palaeozoic corals." He also remarks: "Further, it has long been known that, as such corals gradually reacquire a vertical position, the septal arrangement slowly gives up the bilateral and returns to the radial symmetry. Thus the character on which it was proposed to found a great division of the stony corals was nothing but a slight mechanical adaptation to a passing phase in the life of each individual coral. But it is only fair to say that the whole tendency of recent works on corals has been to discover the invalidity of the supposed division Tetracorallia."

In a previous section (p. 42) I have dwelt upon the significance of bilateral and radial symmetry in corals, and have shown that in both modern and fossil corals the developmental stages throughout are bilateral, and that it is only towards maturity that the most nearly perfect radiality is assumed. It is the order in which the mesenteries and septa appear in corals which gives their distinctive significance to modern and extinct forms, not their bilateral or radial symmetry. Even the first six pairs of mesenteries which arise before any skeleton appears are arranged in a strictly bilateral manner in modern corals, and the subsequent mesenteries and septa also follow the bilateral plan. When fully developed the majority of rugose corals are as perfectly radial as are modern corals. The statement "that the whole tendency of recent work on corals has been to discover the invalidity of the supposed division Tetracorallia" is made on only a partial view of the case. The only recent discovery of any importance in support of Bernard's position is the demonstration, mainly by Miss Ogilvie, of the unity of microscopic structure of the skeleton of rugose and modern corals, a discovery which was to be expected considering that the polyps forming the two groups of skeletons belong to one group, the Zoantharia. Even the discovery by the "Challenger" of the coral *Moseleya*, which, from Quelch's account, was hailed as a living representative of the Tetracoralla, and as breaking down their distinction from living corals, is shown in Bernard's present paper (p. 24) to be alto-

gether unworthy of the importance attached to it, though on grounds which I do not consider the most fundamental. My demonstration that the protoseptal stage of rugose corals is hexameral, like the corresponding stage in modern corals, proves that the Tetracoralla and Hexacoralla are more closely related than has been supposed, even though from this stage they diverge to the same degree as do modern zoanthids and hexactinians. Bernard's assertion is in harmony with others published by Bourne and Ogilvie. In making such these authors have wholly neglected or minimized the significance of the difference in septal sequence between fossil and modern corals, and hitherto it is only such a character which has rendered possible a natural classification of the Anthozoa. Morphologists and systematists know of no character among the Anthozoa of greater value for taxonomic purposes than the mesenterial (and septal) plan. The hexameral protoseptal stage indicates that the tetracorallids and hexacorallids have a common ancestry, but beyond this stage we have no evidence as to their relationships; we have no forms which indicate how the divergence took place, any more than we have for the soft-bodied hexactinians and zoanthids. We cannot think of them as one group derived from the other, but as divergences from a common ancestry.

When this account was practically completed I received three papers from Prof. N. Yakovleff, all devoted to studies of the Rugosa.[1] One, "Ueber die Morphologie und Morphogenie der Rugosa," contains special reference to the subject of the present contribution, and calls for notice. Yakovleff has found that in Russian specimens of *Lophophyllum proliferum* the concave and convex sides of the corallite are the reverse of those in American specimens. In Russian examples the main or ventral-directive septum occurs on the convex side, while in the American it is on the concave side of the coral, the ventral axial fossula varying in

[1] 1. "Die Fauna der oberen Abtheilung der palæozoischen Ablagerungen im Donez-Bassin. II., Die Korallen," Mém. du Comité Géologique, Nouv. Série, Livr. 12, 1903.

2. "A Contribution to the Characteristic of Corals of the Group Rugosa." *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XIII., Feb., 1904.

3. "Ueber die Morphologie und Morphogenie der Rugosa," Ver. der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg, Bd. XLI., Lief. 2, 1904.

like manner. Although in the great majority of rugose corals the ventral-directive septum (Hauptseptum), along with its associated fossula, occurs on the convex border, yet Yakovleff finds the relationship to be occasionally reversed. Such differences the author considers to be a mechanical necessity in the formation of the secondary septa, according as to whether the mouth or oral surface of the living polyp was inclined to one side or the other of the corallite. In the majority of cases it is supposed that the oral disc was inclined towards the concave side, whereas when the ventral directive septum is on the concave side, the polypal disc was directed towards the convex border.

From Yakovleff's account it is evident that various authors have been misled as regards the orientation of the corallite by assuming that the concave and convex borders are morphologically the same throughout. As he points out, the only reliable criteria for purposes of orientation are the relationships of the septa among themselves. Though the axial fossula may occur on either the convex or the concave side of the corallite, it is always associated with the cardinal or ventral-directive septum; the ventral border may be either convex or concave, or indeed at any angle to the concavo-convex axis, according to the species or even individual.

Yakovleff investigates rather fully the claim which has been made for the occurrence of three or four fossulæ in certain species. With regard to *Omphyma* he shows that the presence of more than one depression is doubtful, as also in the genus *Menophyllum*. He concludes for the Rugosa in general that only one fossula, the ventral-directive, is really determinable, the others resting upon insufficient evidence. In support of this he refers to Bernard's statement, already quoted, that he fails to see the evidences for the existence of more that one true fossula in any coral.

In connection with this I would say that whether the alar region with its group of smaller septa, and more or less special interspace, be included within the term fossula is merely a matter of definition. In the forms already referred to (p. 44) such special regions among the septa do occur, and correspond with developmental stages of others in which they are absent at

maturity. They have been described as fossulæ by all writers hitherto, and the purpose of the present paper is to show the true morphological significance both of them and of the axial fossula. It must be admitted, however, that the axial fossula is the only one corresponding with any structural peculiarity (siphonoglyph) of the mature polyp.

It is also incorrect to say that a fossula never occurs on the dorsal border of the corallite in association with the dorsal-directive septum. As mentioned on p. 42, specimens of *Zaphrentis compressa* occasionally show a marked depression in this region, of the same nature as that on the ventral border.

As would be expected, Yakovleff (p. 408) is unable to accept Bernard's explanation of the fossula as due to a bagging down of the basal tissues consequent on the overturning of the protothecа. He also (p. 400) shows the untenable nature of Bernard's view that the bilaterally symmetrical Rugosa have risen from the radially symmetrical Madreporaria as a result of the falling over of the corallite.

Yakovleff (p. 402) evidently shares the general view that the fossulæ are due to the presence of smaller *primary* septa ; " Die Septalgruben sind Viertiefungen, die sich bei den primären Septen befinden . . . in den Septalgruben zeichnen sich die primären Septen gewöhnlich durch ihre schwache Entwickelung (geringen Dimensionen) aus." I have shown above (p. 32) that though the alar fossulæ are always associated with a group of new smaller metasepta yet the primary alar septa (protosepta) are not smaller than the other primary septa ; they form the ventral limit of the alar fossulæ, but themselves take no part in any depression or enlarged interspace. Only the ventral axial fossula has associated with it a smaller primary septum, and this constitutes its fundamental distinction from the lateral depressions.

Summary.

1. The two alar fossulæ present in certain rugose corals correspond with the region of addition of new septa within the middle two of the six primary interseptal spaces, and each is situated on the dorsal aspect of a ventro-lateral or alar septum. The fossula is due to the fact that some of the septa are here shorter,

and are inclined towards and fused in a successive manner with the dorsal older septa.

2. Alar fossulæ indicate with an incomplete stage in the radial development of septa, and similar stages are passed through in the ontogeny of other rugose corals in which the mature calice attains more nearly radial symmetry.

3. The cardinal or ventral-directive fossula where best developed is formed by two distinct structural elements: (*a*) a group of incompletely developed septa on each side of the ventral directive or cardinal septum, and (*b*) a ventral directive or cardinal septum smaller than the other septa of the first cycle.

4. The two ventral groups of incompletely developed septa have a significance similar to that of the alar fossulæ, that is, they represent a developmental stage.

5. The smaller cardinal septum was probably correlated with the presence in the rugose polyp of a ventral siphonoglyph or gonidial groove in the stomodæum, like that which occurs in the living Zoantheæ.

6. In the most radially developed species the simple cardinal fossula is represented by only the shortened directive septum.

7. Like modern corals and cœlenterates generally all the Rugosa exhibit bilateral symmetry during their development, and as they approach maturity they become more or less radial.

8. The bilaterality and radiality of tetracorallids and hexacorallids are of very different origin and character, and along with other characteristics of the two groups do not imply any relationship beyond the protoseptal stage.

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